

HABITAT FRAGMENTATION IN THE TEMPERATE ZONE

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In this chapter we examine three questions relating to habitat fragmentation in the temperate zone: (1) What is the effect of fragmentation on the species originally present in the intact habitat? (2) How does fragmentation lead to the loss of species? (3) For an already fragmented landscape, are there any guidelines for the selection and management of nature reserves? Here we shall set as our goal the long-term preservation of those species whose continued existence is jeopardized by habitat destruction. At the outset we note that this chapter is slanted towards vertebrate communities (especially birds) and forested habitats. Our bias reflects, in part, a bias in the existing literature. On the other hand, by virtue of their low population densities, birds and mammals are among the taxa most likely to disappear from isolated fragments (Wilcox, 1980).

INTRODUCTION

Fragmentation occurs when a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original. When the landscape surrounding the fragments is inhospitable to species of the original habitat, and when dispersal is low, remnant patches can be considered true "habitat islands," and local communities will be "isolates" (*sensu* Preston, 1962). If the matrix can support populations of many of the species from the original habitat, or if dispersal between patches is high, communities in the fragments will effectively be "sam-

ples" from the regional faunal or floral "universe" (Preston, 1962; Connor and McCoy, 1979). The process of isolate formation through fragmentation has been termed "insularization" by Wilcox (1980). The challenge to conservationists is to preserve as much of the species pool as possible within these fragments, in the face of continual habitat destruction.

Habitat fragmentation has two components, both of which cause extinctions: (1) reduction in total habitat area (which primarily affects population sizes and thus extinction rates); and (2) redistribution of the remaining area into disjunct fragments (which primarily affects dispersal and thus immigration rates). Both Lovejoy et al. (1984) and Haila and Hanski (1984) stress the need to partition extinctions into those caused purely by habitat destruction and those in which insularization is an important additional component.

Temperate communities are widely believed to be more resistant to the effects of habitat fragmentation than are tropical communities. Temperate species tend to occur in higher densities, be more widely distributed, and have better dispersal powers than their tropical counterparts. These attributes should allow populations to persist in smaller patches of suitable habitat. Although local extinction rates may be high (due to high levels of population fluctuation and shorter individual lifespans; see Diamond, 1984a), high vagility can facilitate rapid recolonization from other fragments following extinction (Brown and Kodric-Brown, 1977).

On the other hand, one of the main reasons why habitat fragmentation seems less severe in the temperate zone is that most of the damage was done long before most people were aware of it. For example, in Great Britain reduction and fragmentation of the original forest cover began some 5000 years ago with permanent clearances by Neolithic farmers, and was well advanced by the time of the Norman Conquest in 1066 (Figure 1). Species whose extinctions in Great Britain were certainly related to the destruction of the original forest (as well as other causes, especially hunting) include: brown bear (extinct by the time of the Norman Conquest), wild boar (18th century), wolf (18th century), goshawk (19th century; now reestablished in new conifer plantations), and capercaillie (18th century; now reintroduced in new conifer plantations).

Much the same story can be told for the fauna of the deciduous forest of the eastern United States, where widespread forest destruction began with the arrival of European settlers (about 300 years ago) and reached a peak about the time of the Civil War. Here, too, a number of species vanished from the east as a result of habitat destruction combined with hunting. These include wolf (19th century), mountain lion (20th century, although a few persist in Florida), elk

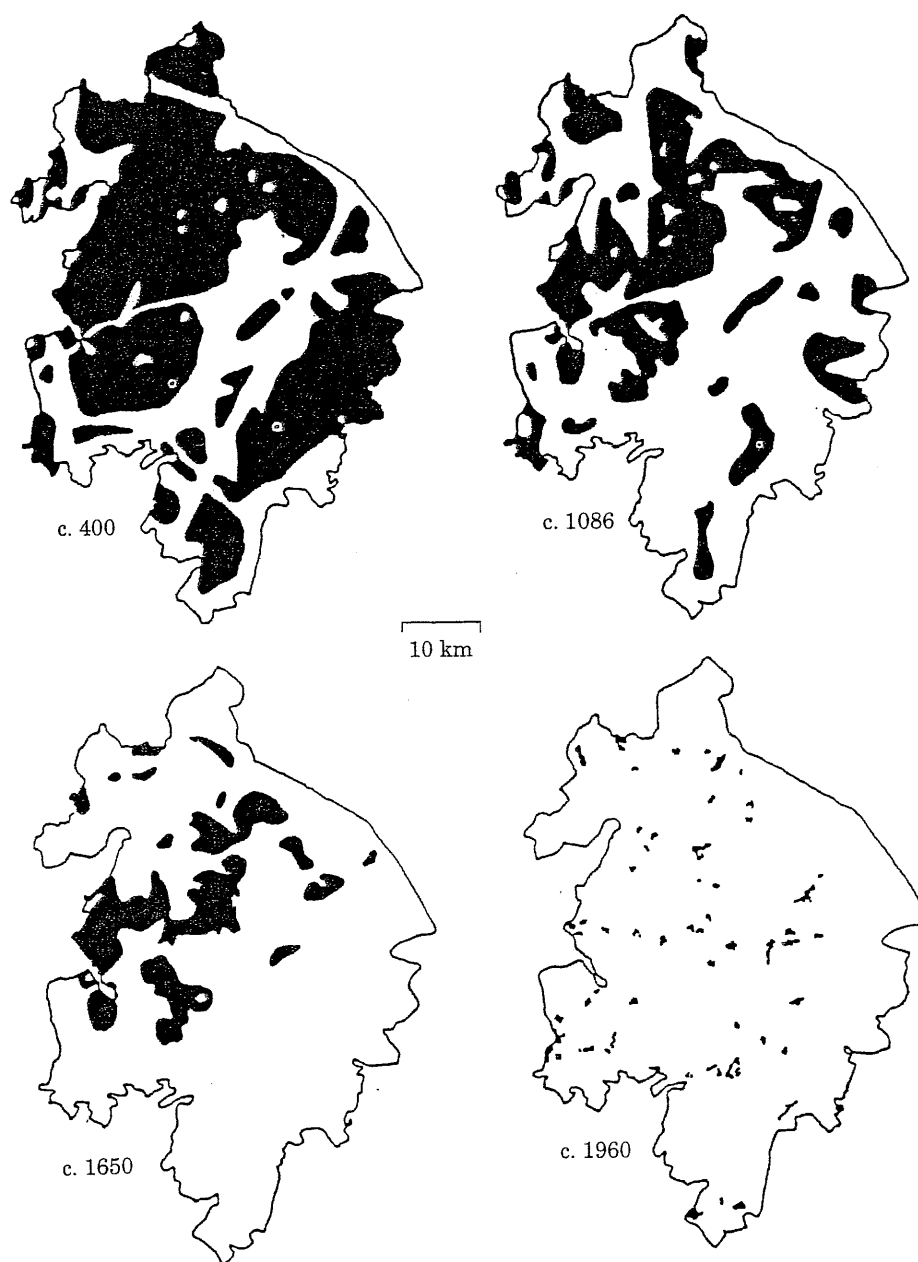


FIGURE 1. Forest fragmentation in Warwickshire, England, from 400–1960 A.D. Forested areas are shown in black. (Redrawn from Thorpe 1978.)

(19th century), passenger pigeon (20th century), and ivory-billed woodpecker (20th century). For both the British and American species, it is probably correct to say that even if they could be reintroduced to their former haunts, the outcome would be disappointing: suitable habitat no longer exists.

The species that survived this initial round of habitat fragmentation were the ones better able to withstand the human impact on the landscape, but by no means is the problem over. In Great Britain today, pressure on the land is so great that many of the "semi-natural" habitats which replaced the original forest are themselves severely reduced and fragmented. Examples include lowland heaths (Moore, 1962; Webb and Haskins, 1980), upland moors (Porchester, 1977; Parry et al., 1981) and calcareous grasslands (Blackwood and Tubbs, 1970; Jones, 1973). There is now a growing list of species characteristic of, or restricted to, these habitats whose declines or extinctions can be attributed at least in part to fragmentation (see Hawkesworth, 1974 for a general survey). In the United States, the continuing fragmentation of such habitats as old-growth Douglas fir forests in the Pacific northwest (Harris, 1984), deciduous forests in the east (Burgess and Sharpe, 1981; Whitcomb et al., 1981), and grasslands in the midwest has prompted concern for the continued survival of the species that inhabit them (including small whorled pogonia, greater prairie chicken, spotted owl, and Delmarva fox squirrel). Fragmentation remains the principal threat to most species in the temperate zone.

A MODEL OF FRAGMENTATION

Analyses of the effect of fragmentation (and guidelines for the design of nature reserves) have generally been based on the conceptual framework of island biogeography (Preston, 1962; MacArthur and Wilson, 1967; Soulé and Wilcox, 1980; Burgess and Sharpe, 1981). This theory suggests that the number of species on an oceanic island represents a balance, or dynamic equilibrium, between processes of immigration and extinction. The equilibrium number of species on an island depends upon the characteristics of the island—in particular, its size and isolation from potential sources of colonists—and the characteristics of the species themselves—in particular, their dispersal abilities and population densities.

We have recently (McLellan et al., 1986) developed a computer model that simulates the effects of habitat fragmentation on two pools of species with different minimum area requirements and dispersal abilities. This model has led to a number of insights regarding the extent of fragmentation that different species can tolerate.

TABLE 1. Scientific names of plants and animals mentioned in the chapter.

<i>Plants</i>	Dog's mercury: <i>Mercurialis perennis</i> Small whorled pogonia: <i>Isotria medeoloides</i>
<i>Insects</i>	Large blue butterfly: <i>Maculinea arion</i>
<i>Amphibians</i>	Red-spotted newt: <i>Notophthalmus viridescens</i>
<i>Birds</i>	American woodcock: <i>Scolopax minor</i> Blue-gray gnatcatcher: <i>Polioptila caerulea</i> Blue jay: <i>Cyanocitta cristata</i> Brown-headed cowbird: <i>Molothrus ater</i> Capercaillie: <i>Tetrao urogallus</i> Common grackle: <i>Quiscalus quiscula</i> Goshawk: <i>Accipiter gentilis</i> Greater prairie chicken: <i>Tympanuchus cupido</i> Great spotted woodpecker: <i>Picoides major</i> Ivory-billed woodpecker: <i>Campephilus principalis</i> Kirtland's warbler: <i>Dendroica kirtlandii</i> Louisiana waterthrush: <i>Seiurus motacilla</i> Passenger pigeon: <i>Ectopistes migratorius</i> Spotted owl: <i>Strix occidentalis</i>
<i>Mammals</i>	Bobcat: <i>Lynx rufus</i> Brown bear: <i>Ursus arctos</i> Delmarva fox squirrel: <i>Sciurus niger cinereus</i> Eastern chipmunk: <i>Tamias striatus</i> Elk: <i>Cervus elaphus</i> Gray squirrel: <i>Sciurus carolinensis</i> Mountain lion: <i>Felis concolor</i> Opossum: <i>Didelphis virginiana</i> Raccoon: <i>Procyon lotor</i> Short-tailed weasel: <i>Mustela erminea</i> White-tailed deer: <i>Odocoileus virginianus</i> Wild boar: <i>Sus scrofa</i> Wolf: <i>Canis lupus</i>

The pattern of fragmentation of our hypothetical habitat is based largely on that of heathland in Dorset, England, as reported by Moore (1962) and Webb and Haskins (1980). In our model, the original habitat is reduced from five extremely large tracts to an archipelago of over 450 fragments totalling 5 percent of the original area. For simplicity we have shown the total area of habitat decreasing linearly over time; in reality, the rate of destruction usually increases with time. The total number of fragments increases exponentially over time, reflecting a distribution increasingly skewed towards a large number of very small fragments (Figure 2). At each stage of fragmen-

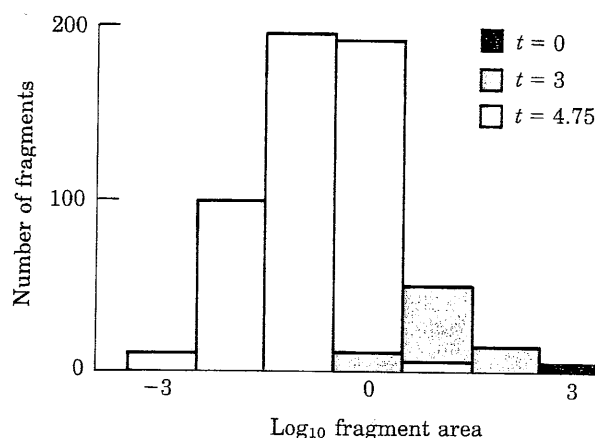


FIGURE 2. The frequency distributions of fragment sizes at various stages of the fragmentation sequence. The top diagram corresponds to the original ($t = 0$), largely contiguous habitat. Fragmentation results in a larger number of smaller patches (lower diagrams) with a total area less than that of the original habitat. (From McLellan et al., 1986.)

tation, the remaining area of habitat is distributed among the growing number of fragments in a roughly lognormal fashion. There is no information on interfragment distances for the heathlands, so we have borrowed a pattern from another system, namely woodland in Cadiz township, Wisconsin. Sharpe et al. (1981) have shown that mean nearest-neighbor distances increased until about 10 percent of the original area was left, and then remained constant despite further losses.

Details of the model

The two species pools were chosen to represent the extremes of susceptibility to fragmentation: one (resistant) pool consisted of species with good dispersal abilities and a low average proneness to local extinction. The other (susceptible) pool had species with poor dispersal abilities and a high average proneness to local extinction. The results therefore define qualitatively the range of patterns of species loss to be expected in habitats undergoing fragmentation. The fates of the P species in each pool were modeled using a species-by-species ("molecular"; see Gilpin and Diamond, 1981) formulation of the equilibrium model. The basic variable is the probability J_i that a given species i ($i = 1, 2 \dots P$) occurs as a breeding population in a fragment. This probability, termed the "incidence" (Diamond, 1975a) of the species, increases with fragment area (A), due to increasing population size and thus decreasing chance of stochastic extinction, and decreases

with distance (D) from a source of colonists due to decreasing frequency of immigration. Observed values of J_i plotted against area for a given distance, or vice versa, are called "incidence functions" (Diamond, 1975a; Figure 3). Elaborations such as dependence of extinction rates on distance (due to the "rescue effect;" see Brown and Kodric-Brown, 1977) and dependence of immigration rates on area (due, for example, to "passive sampling;" see Connor and McCoy, 1979) are not incorporated in this model.

This model has the general form

$$\frac{dJ_i}{dt} = I_i - E_i \quad (1)$$

where I_i is the net rate at which unoccupied fragments are colonized by species i and E_i is the net rate at which the species becomes locally extinct. We chose to use a version of this general model first presented by Levins and Culver (1971):

$$\frac{dJ_i}{dt} = a_i J_i (1 - J_i) - b_i J_i \quad (2)$$

where a_i is an instantaneous colonization rate per occupied fragment and e_i is an instantaneous local extinction rate. This model differs from the version described by Gilpin and Diamond (1981) in that the instantaneous rate of colonization of unoccupied fragments ($a_i J_i$) is a

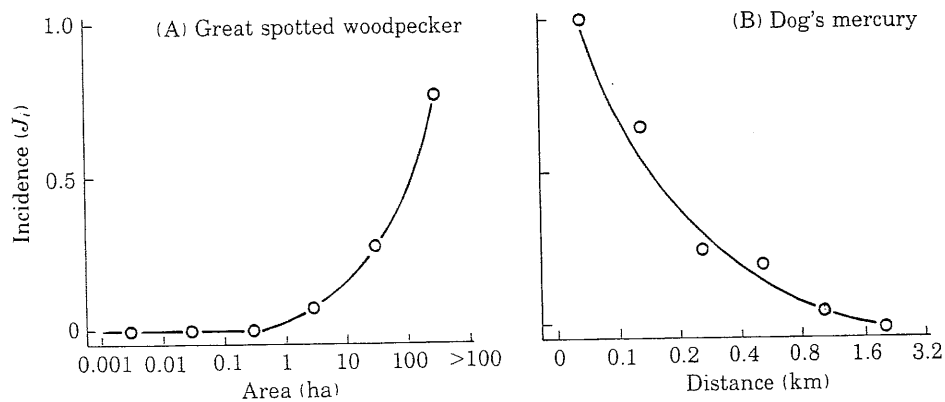


FIGURE 3. Incidence functions for two species in forest fragments in Britain. (A) Incidence (J_i , the proportion of woods in each class occupied by a population) of the great spotted woodpecker plotted against woodland area. (From Moore and Hooper, 1975.) (B) Incidence of dog's mercury, a woodland herb, in secondary forest in Lincolnshire plotted against the distance to the nearest older forest containing the species. (From Peterken and Game, 1981). Curves were drawn by eye.

function of J_i rather than a constant. This is more appropriate for fragmented systems, where colonists must come from other (occupied) fragments rather than from some large, inviolate, "mainland" area. At equilibrium I_i and E_i are equal, and J_i is constant at the equilibrium incidence level J_i^* . For equation (2) this is

$$J_i^* = 1 - \frac{b_i}{a_i} \quad (3)$$

Thus incidence is positive only when the colonization rate (a_i) exceeds the extinction rate (b_i).

Incidence functions were generated by specifying the dependence of a_i on distance and b_i on area. We used an exponential function for $a_i = f(D)$

$$a_i = c_i \cdot \exp \frac{-D}{D_i} \quad (4)$$

where c_i is a colonization coefficient and $1/D_i$ the death rate per unit distance of migrants (Gilpin and Diamond, 1976). An inverse hyperbolic function was used for $b_i = f(A)$

$$b_i = e_i/A \quad (5)$$

where e_i is an extinction coefficient (Gilpin and Diamond, 1976). Substituting equations (4) and (5) into equation (3) gives the expression for J_i^* as a function of area and distance

$$J_i^* = 1 - \left[\frac{e_i}{c_i} \cdot \exp \frac{D/D_i}{A} \right] \quad (6)$$

When $D/D_i \approx 0$ (i.e., in nonisolated fragments), equation 6 describes a hyperbolic function with increasing area, with the parameter e_i/c_i corresponding to the area at which incidence is zero. We distributed this "minimum area" lognormally with variance 1.0 in each of the species pools, with the susceptible pool having a mean value an order of magnitude greater than the resistant one. (For theoretical justification of the lognormal in such models see Gilpin and Armstrong, 1981, and for empirical evidence see Gilpin and Diamond, 1981.) For a given area, equation (6) describes an exponential function with the parameter D_i (the "mean dispersal distance;" see Gilpin and Diamond, 1976) corresponding to the distance required to reduce J_i to $1/e$ (36.8%) of its values at $D = 0$. We treated D_i unrealistically as constant among species in a given pool, assigning the susceptible pool a value half that given to the resistant pool.

Results of the model

The results of this exercise are illustrated in Figure 4. Initially, when a large amount of habitat remains, mostly in large fragments, few or no species are lost from either pool. As fragmentation proceeds we eventually reach some critical level of reduction and fragmentation where species begin to die out. The susceptible pool loses species earlier and loses more species in total than does the resistant pool. When the resistant pool begins to lose species, it loses them very rapidly, because by this time the fragments are small and there is little habitat left.

Insularization causes extinctions over and above those expected through reduction in the total area of habitat. More species persist at equilibrium if the remaining habitat is concentrated into a single large patch rather than distributed over many small fragments (Figure 4). We stress that the results in Figure 4 are equilibrium patterns; depending on the relative time scales of habitat destruction and species'

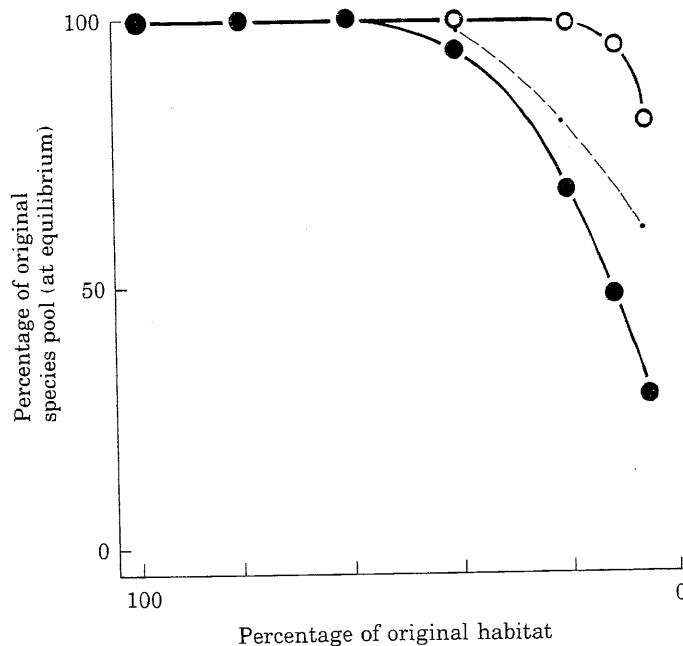


FIGURE 4. The number of species remaining in each species pool as fragmentation proceeds. Closed circles show the pool of species with large area requirements and low vagility. Open circles show the species with less stringent area requirements. The small dots connected by the dashed line depict the proportion of the first pool that would be present when the habitat is minimally fragmented. (From McLellan et al., 1986.)

population dynamics, extinctions may either closely track the changing landscape patterns or lag behind them.

An important omission from the model is the explicit inclusion of population size as a variable (see Schoener, 1976; Williamson, 1981). Species' carrying capacities are assumed to be directly proportional to fragment size, and extinctions simply the result of demographic stochasticity. It seems more likely both that habitat heterogeneity means that the carrying capacity is not a simple function of area, and that factors like environmental stochasticity and population structure are important in determining extinction rates (see MacArthur and Wilson, 1967; Richter-Dyn and Goel, 1972; Leigh, 1975, 1981 for details; Diamond, 1984a; and Gilpin and Soulé, Chapter 2 for a summary). Colonization will also be affected by habitat heterogeneity and population dynamics. If a fragment does not contain enough suitable habitat for a given species, establishment of a breeding population will not occur no matter how high the immigration rate. Similarly, abundant species will produce more colonists than scarce ones. Such factors will need to be included in more realistic (albeit more complex) models.

Despite these limitations, we believe the model provides a clear message: Even where most of the habitat has already been destroyed, subsequent fragmentation should be minimized, lest a rapid loss of species occur. Furthermore, insularization can cause extinctions independent of habitat reduction.

MECHANISMS OF EXTINCTION

The above theoretical discussion has taken something of a black box approach to fragmentation. In this section, we shall focus on the proximate mechanisms of extinction. These include home range size, loss of habitat heterogeneity, effects of habitats surrounding fragments, edge effects, and secondary extinctions.

Home range

Some fragments will be smaller than the minimum home ranges or territories of certain species. This is often the case for large animals. For example, a single pair of ivory-billed woodpeckers may require 6.5–7.6 km² of undisturbed bottomland forest (Tanner, 1942). The European goshawk has a home range of approximately 30–50 km² (Cramp and Simmons, 1979). Male mountain lions in the western United States may have home ranges in excess of 400 km² (Seidensticker et al., 1973). However, species often disappear from habitat fragments that far exceed their minimum home range sizes; mecha-

nisms other than home range limitations must be operating in such cases.

Loss of habitat heterogeneity

One common consequence of fragmentation is a loss of habitat heterogeneity. Even a seemingly uniform expanse of habitat such as forest or grassland is, at some level of discrimination, really a mosaic of different habitats. Individual fragments may lack the full range of habitats found in the original block. Patchily distributed species or species that utilize a range of microhabitats are especially vulnerable to extirpation under these circumstances. An example of such a patchily distributed species is the Louisiana waterthrush of eastern North America. It nests and forages near open water, especially fast-moving streams (Chapman, 1907). Woodlots without open water do not provide suitable habitat for the waterthrush, and, not surprisingly, this bird is one of a number of forest songbirds that are rarely encountered in small woodlots (Robbins, 1980).

While the habitat requirements for most songbirds are far less obvious, they may nonetheless play a major role in the response of these birds to fragmentation. Lynch and Whigham (1984) studied the bird communities and vegetation of 270 woodlots in Maryland. They discovered that structural or floristic characteristics of the vegetation strongly influenced the local abundance of each bird species. These vegetation characteristics, in turn, varied with the forest size. A qualitatively similar result was noted by Bond (1957) in forest fragments in southern Wisconsin. Although generalizations are risky, we might expect this problem of patchiness to be most acute for plants, and for insects that depend upon specific host plants.

When species require two or more habitat types, fragmentation may make it impossible for them to move between habitats. Karr (1982a) has attributed many of the extinctions of landbirds of Barro Colorado Island, Panama to just this mechanism. Within the temperate zone, this problem is likely to befall many kinds of organisms. The red-spotted newt is typical of a number of amphibians in having both a terrestrial and an aquatic stage. The terrestrial efts may remain ashore for up to three years, but eventually must return to the water to breed. Among birds, the blue-gray gnatcatcher in California moves from deciduous oak woodlands to chaparral and live oaks over the course of the breeding season (Root, 1967). Other temperate zone birds are also believed to make seasonal shifts in their ranging behavior (MacClintock et al., 1977). Unfortunately, too little is known about the behavior of most temperate zone animals to say with certainty what their habitat requirements are, or how these requirements may

change seasonally. This lack of knowledge is always an obstacle to predicting the effects of fragmentation on individual species. Detailed information on habitat usage will be crucial to devising successful conservation programs for many species.

Effects of habitat between fragments

In the case of a true island, the ocean is an impassive barrier, and potential colonists will either traverse it successfully or perish in the attempt. In the case of a habitat fragment, the ocean has been replaced by a landscape of human dwellings or agricultural land. This landscape can also be a formidable barrier to colonists from the fragments. Unlike an ocean, however, a human-created landscape can contribute directly to the extinction of species within fragments. It does so by building up populations of animals that are harmful to species within the fragments. A good example of this problem comes from studies of forest-dwelling songbirds in forest fragments in the eastern United States.

Breeding populations of songbirds have been declining in small woodlots throughout the eastern United States since the late 1940s (Robbins, 1979; Whitcomb et al., 1981; Wilcove, 1985a). A number of factors have contributed to this decline, two of the most important being high rates of nest predation (Wilcove, 1985b) and brood parasitism by the brown-headed cowbird (Mayfield, 1977; Brittingham and Temple, 1983). In recent decades, the numbers of nest predators and cowbirds have increased greatly as a result of human-induced changes in the landscape.

Among the nest predators, blue jays, raccoons, and gray squirrels all occur in higher densities in suburban communities than in more natural habitats like forests (Flyger, 1970; Fretwell, 1972; Hoffman and Gottschang, 1977). Prior to the arrival of European settlers, the cowbird was largely confined to the grasslands of the midcontinent, where it followed the grazing mammals and ate the insects they stirred up. With the disruption of the eastern deciduous forest and the introduction of livestock, the cowbird spread throughout the eastern United States and Canada (Mayfield, 1977). More recently, the cowbird population in eastern North America has increased tremendously due to an increase in their winter food supply—waste grain in southern rice fields (Brittingham and Temple, 1983). The advent of mechanical harvesters has simultaneously increased the amount of land under rice cultivation and the amount of waste grain. This range expansion and population increase has brought the cowbird in contact with popula-

tions of forest-dwelling songbirds, most of which lack behavioral defenses against cowbird parasitism (Rothstein, 1975; May and Robinson, 1985).

No habitat preserve is immune to the effects of human activity outside its borders, and wildlife managers must concern themselves with the ecological effects of land development outside the boundaries of protected areas. To quote Janzen (1983), "No park is an island."

Edge effects

Wildlife managers have long extolled the virtues of forest edge (see for example Dasmann, 1964, 1971; Yoakum and Dasmann, 1969; Burger, 1973), in a tradition dating back to the writings of Aldo Leopold (1933). Certainly a variety of game animals, including white-tailed deer and American woodcock, do well in edge habitats. But it is becoming increasingly clear that the forest edge has a strong negative impact on other members of the woodland flora and fauna (Hubbell and Foster, Chapter 10; Lovejoy et al., Chapter 12; Janzen, Chapter 13).

Ranney et al. (1981) believe that the seed rain into the cores of small woodlots is dominated by the seeds of the edge species. This may ultimately change the species composition of the woodlots, as the shade tolerant plants of the interior are replaced by shade intolerant forms from the edge. Such an effect would require the number of plants germinating to vary with the number of seeds set in the interior. Ranney et al. note that very small or irregularly shaped forest reserves may be unable to sustain populations of forest interior plants.

Field studies by Gates and Gysel (1978), Chasko and Gates (1982), and Brittingham and Temple (1983) have shown that the nesting success of songbirds is lower near the forest edges than in the interior (Figure 5). This is because many nest predators (blue jay, American crow, common grackle, eastern chipmunk, short-tailed weasel, raccoon) and brood parasites (brown-headed cowbird) occur in higher densities around forest edges (Bider, 1968; Robbins, 1980; Whitcomb et al., 1981; Brittingham and Temple, 1983).

For management purposes, it is important to know how far into the forest the influence of the edge is felt. Studies by Ranney (1977) and Wales (1972) show that the major vegetational changes caused by the edge extend only 10–30 m inside the forest, depending on whether the edge has a northerly or a southerly exposure. However, by placing artificial nests at varying distances from the edge, Wilcove (1985a) has shown that the edge-related increase in predation may extend from 300–600 m inside the forest (Figure 6). It should not be surprising

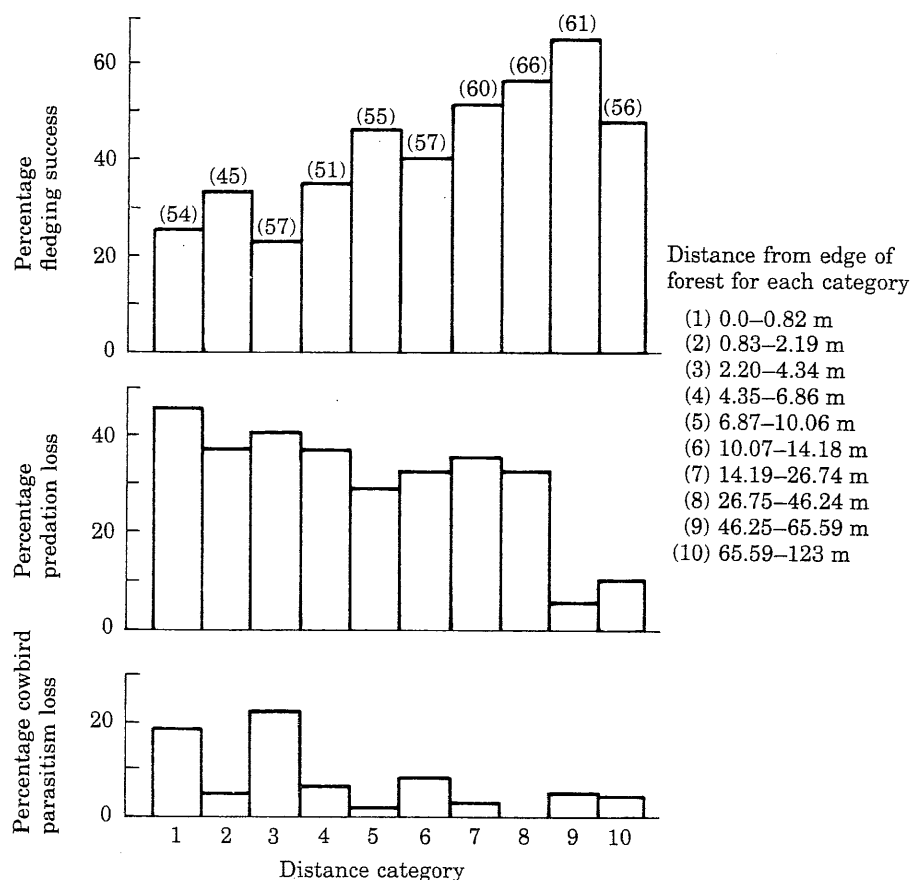


FIGURE 5. Nesting success of songbirds as a function of distance from the forest edge, based on a study in Michigan. Distance categories 1–10 are delimited at right, sample sizes are in parentheses. (From Gates and Gysel, 1978.)

that the faunal effects of a forest edge would exceed the floral effects. Birds like crows, grackles, and cowbirds are not intolerant of the forest interior. Similarly, mammals like the raccoon, weasel, and chipmunk, while concentrating their activities near the forest edge, will also frequent the forest interior (Whitaker, 1980).

One consequence of these observations deserves special emphasis: if 600 m is taken as a liberal estimate of the faunal edge effect, then circular reserves smaller than 100 ha will contain no true forest interior. In the case of forest songbirds, this finding suggests that reserves should contain *at least* several hundred ha of uninterrupted forest. In fact, far larger areas may be needed to ensure the long term survival of these birds (Whitcomb et al., 1976).

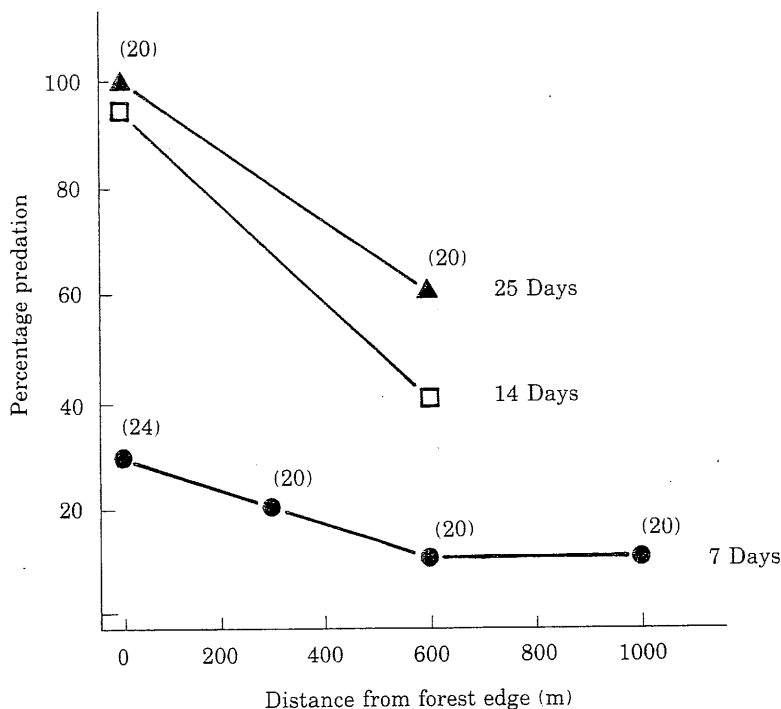


FIGURE 6. Percentage of experimental nests preyed upon as a function of distance from the forest edge. Nests are wicker, open-cup baskets containing fresh quail eggs. Solid circles are the predation rates after 7 days, open squares are after 14 days, and closed triangles are after 25 days. The numbers in parentheses are the numbers of experimental nests. The data suggest that the edge-related increase in predation may extend from 300–600 m inside the forest. (From Wilcove, 1985a.)

Secondary extinctions

Fragmentation often disrupts many of the important ecological interactions of a community, including predator–prey, parasite–host, and plant–pollinator relations, and mutualisms (Gilbert, 1980; Terborgh and Winter, 1980). The disruption of these interactions may lead to additional extinctions, sometimes referred to as “secondary extinctions.” Typically, these secondary extinctions are associated with the decay of complex tropical communities, but they are certainly not unknown in the temperate zone. For example, small woodlots in the eastern United States support few, if any, large predators like mountain lions, bobcats, and large hawks or owls that may regulate populations of smaller, omnivorous species like raccoons, opossums, squirrels, and blue jays (Matthiae and Stearns, 1981; Whitcomb et al.,

1981). These omnivores, in turn, prey upon the eggs and nestlings of the forest songbirds. As noted earlier, the rate of nest predation in small woodlots is very high, and this may be one reason why songbird populations have declined. A similar explanation has been invoked to explain some of the avian extinctions on Barro Colorado Island, Panama (Terborgh, 1974).

A more complicated example involves the extinction of the large blue butterfly in Britain (Thomas, 1976; Ratcliffe, 1979). This butterfly has a remarkable life history in that the larvae must develop within the nests of the red ant *Myrmica sabuleti*. The large blue was brought to the brink of extinction when land development and reduced grazing by livestock eliminated the open areas it required. The remaining populations vanished through a complex chain of events. An epidemic of myxomatosis in the mid-1950s depressed rabbit populations, and as a result many of the sites became overgrown with scrub. The *Myrmica sabuleti* ants were unable to survive in the overgrown areas, and their decline meant the end of the large blue.

We suspect that as more data on fragmentation are gathered, secondary extinctions will prove a common occurrence in temperate communities. The prevention of these extinctions will require synecological studies involving threatened species, coupled with active management of preserves.

GUIDELINES FOR TEMPERATE ZONE RESERVES

Although blanket prescriptions for the design of nature reserves (Wilson and Willis, 1975; Diamond, 1975b) have come under criticism in recent years (examples include Simberloff and Abele, 1976; Abele and Connor, 1979; Higgs and Usher, 1980; Game, 1980; Margules et al., 1982; Boeklen and Gotelli, 1984), we believe that the theory of island biogeography provides a useful framework within which more detailed studies of particular cases can be planned. In this final section, we focus on three questions:

1. How much of the available habitat must be set aside as reserves, and in what distribution of sizes?
2. Should reserves be clustered together in close proximity to each other, or spread out over a broad area?
3. What is the optimum shape for reserves?

It is important to realize that the "correct" answers to these questions may depend very much on the scale of the conservation effort, because local, regional, and national conservation operations usually operate under very different budget constraints and spatial scales. Once again,

we note that our perspective on these questions is rather ornithocentric.

How much and how large?

A characteristic pattern in habitats undergoing fragmentation is an increasingly skewed distribution of fragment sizes as the total area of habitat declines. In general, a large proportion of the remaining area of highly fragmented habitats should be targeted for protection in order to avert (or at least minimize) the biotic collapse which models suggest can occur in such systems. All other things being equal, priority should go to the largest remaining fragments, for several reasons. First, as emphasized in our model, different species have different area requirements, and the large fragments will often be the only refuge for species which exist at low densities (such as top predators and large herbivores) or who are habitat specialists whose requirements are only satisfied in large areas. Second, the large fragments may well serve as sources of immigrants for marginal populations in neighboring small fragments. If many species are maintained in these small fragments by the "rescue effect" (Brown and Kodric-Brown, 1977), then the small fragments do not represent a viable reserve strategy on their own (although they may be useful in an integrated regional strategy; see below). Third, the trend will always be for large fragments to be eroded unless protected. Because of the cost involved, the responsibility for acquiring and managing these large reserves must rest primarily with national conservation organizations.

The foregoing discussion is not meant to denigrate the value of small reserves. Indeed, their selection emerges as a logical strategy when one considers the different levels of organization and scale at which conservation policy is determined (McLellan et al., 1986). We have argued above that the largest fragments of threatened habitats should generally be obtained as reserves by *national* conservation organizations. However, in a heterogeneous environment these reserves may not encompass all of the habitat variation (and thus all of the characteristic biota) present in the ecosystems concerned. Thus, we suggest the primary task for conservation organizations operating on a *regional* scale should be to distribute their funds for land acquisition among a series of medium sized reserves designed to capture this variation. The optimal trade-off between capturing more habitat heterogeneity (by purchasing several smaller reserves) and maintaining viable populations of area-sensitive species (by purchasing fewer larger reserves) will have to be determined by detailed studies of each particular system (Simberloff and Abele, 1982). Conservation on a *local* scale, as in a township, operates under the tightest budgetary

constraints and thus the most restricted size range for possible reserves (all of which will be small in absolute terms). However, it is possible to state with some confidence that the best strategy at this scale is to go for single "large" reserves rather than several (very) small ones. There are two main reasons: (1) The slope (z) of the species-area relationship is normally steep (>0.35) at small areas where fragments contain a small proportion (<0.25) of the species pool (Martin, 1981); (2) The similarity in species composition among the small local reserves will usually be very high ($>>0.5$) because of their physical proximity and likely similarity in habitat, and because the effective species pool which can colonize them may be considerably less than the regional pool due to minimum area effects. Higgs and Usher (1980) have shown that under these circumstances more species will be contained in single large reserves (Figure 7).

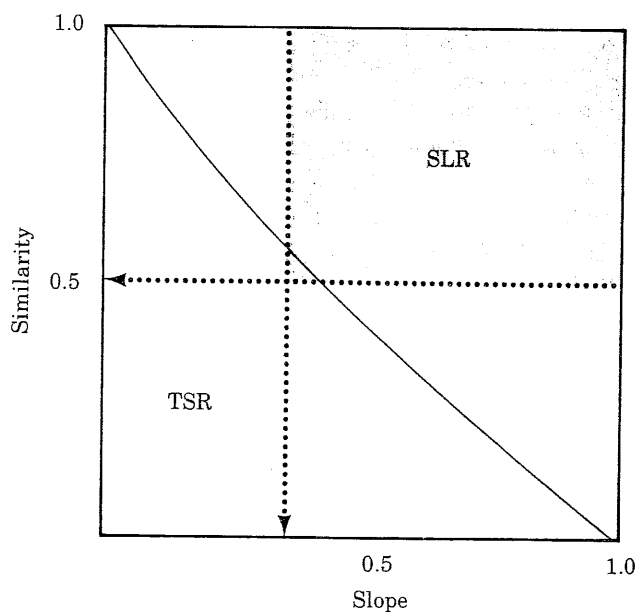


FIGURE 7. This diagram shows how the similarity in species composition (Jaccard's coefficient) between two equal-sized small reserves and the slope of the (log-log transformed) species-area relationship determine whether or not more species will be preserved in one large area or two smaller areas of the same total area. Above the solid line, a single large reserve (SLR) holds more species; below it two small reserves (TSR) hold more species. The dotted lines and shaded area define the expected parameter space when the SLR is small in absolute terms, and all of the reserves are geographically close (i.e. when conservation is operating on a local scale). (After Higgs and Usher, 1980.)

For each major habitat type within a given region, the result of applying these hierarchical strategies would be a small number of large national reserves, a network of medium-sized regional reserves, and a large number of small local reserves. With sufficient integration between organizational levels, primarily in regard to reserve placement (see below), a composite strategy such as this might be adequate to ensure the long-term persistence of those target species not already extirpated by fragmentation.

How close?

It will often be impractical to speak of clustering large national reserves such as national parks and forests, since they can be in widely separated regions of the country. On a local level, there may be great benefit to placing reserves close to each other. The large national preserves can serve as sources of colonists for the smaller local preserves, which themselves may serve reciprocally as stepping stones. These benefits will accrue only to the more vagile organisms such as birds (Lynch and Whigham, 1984), bats (Wilcox, 1980), and those species able to pass through the variety of habitats in the surrounding landscape (many temperate zone mammals). In terms of linking reserves, the value of corridors *per se* is debatable. They are unlikely to reduce the isolation of two distant reserves, and dispersal might occur anyhow if the reserves are close (Frankel and Soulé, 1981). More useful are land use practices which allow populations of many target species to exist at least marginally in the surrounding habitat. These populations can then diffuse into the reserves.

Reserve shape

Diamond (1975b) and Wilson and Willis (1975) have recommended that reserves be as nearly circular in shape as possible. The stated reason is to minimize dispersal distances within a reserve (but see Game, 1980). In the case of temperate zone forest reserves, we may add a second reason—to minimize the proportion of forest edge to forest interior. (By similar reasoning, clearings should not be allowed within the forest. If clearings must be created, they should be placed as close to the edge as possible and clustered together.)

Blouin and Connor (1985) have produced a detailed statistical analysis of data for oceanic islands which suggests that island shape is unimportant in determining the species composition of the islands studied. However, the analysis misses the point about application of the theory of island biogeography to the management of species in nature reserves. Essentially, circularity in the shape of forest frag-

ments may be advocated purely to diminish the impact of edge effects. This is unlikely to be important in oceanic island habitats, where interactions between species across the border of the island are very infrequent. Indeed, at the risk of overgeneralizing, we suggest that the optimal shape for *any* habitat reserve is circular, so as to minimize contact between the protected interior and the surrounding habitat.

Management

Finally, we believe that over the long run virtually all temperate zone reserves will require active management to prevent or overcome the ecological imbalance created by fragmentation or human activity. Good reserve design will lessen but rarely eliminate the need for management (Gilbert, 1980). Such management may take several forms, including controlled treatment of the vegetation to preserve particular successional stages (open country for the large blue butterfly); the elimination of foreign species (wild boars in the Great Smoky Mountains National Park); or the culling of populations of "nuisance" animals (cowbirds in the breeding grounds of the Kirtland's warbler). Conservationists must realize that the battle is not over once the land has been saved. Indeed, it has just begun.

SUGGESTED READINGS

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